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ADAPTATION TO AQUATIC, ARBOREAL, FOSSORIAL AND CURSORIAL HABITS IN MAMMALS.[1]

I. AQUATIC ADAPTATIONS.

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THERE seems to be no doubt whatever that all mammals were originally terrestrial animals. However, either the abundance of food occurring in the water or the competition existing on the land has from time to time led or driven many species to an

[1] In the *American Naturalist* of May, 1902, I published an article entitled "The Law of Adaptive Radiation," a development of the idea of divergent evolution as applied to the larger and smaller groups of mammals. There was considered first, *general adaptive radiation* including the radiation of marsupials and the six independent radiations of the Placentalia, second the law of *local adaptive radiation* and finally the bearing of adaptive radiation on Cuvier's *law of correlation*. Pursuing this general idea of adaptive radiation it appeared desirable to reëxamine and compare the mammals as to the adaptations of different kinds which arise independently in different groups, in other words the *parallel adaptations*.

A number of advanced students of the evolution of mammals undertook this comparison and the results were so interesting and in many cases so novel that they appeared worthy of publication in the *American Naturalist*. They form the basis of the three or four articles which the *Naturalist* will publish successively.

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aquatic life. The following list, though making no pretensions to completeness, will serve to indicate how great and varied a number of forms have become, either from choice or necessity, more or less aquatic.

Cetacea, the entire order.
Sirenia, the entire order.
Carnivora,
  Pinnipedia, the entire suborder.
  Fissipedia,
    Lutra, the various species of otters.
    Enhydris (Latax), the sea-otter.
    Putorius, the mink and sumpfotter.
Rodentia, many scattered examples, as —
    Myocastor (Myopotamus).
    Hydrochœrus, the capybara.
    Hydromys, the Australian water-rat.
    Hydrochilus.
    Microtus (Arvicola) the water-vole.
    Ichthyomys.
    Castor, the beavers.
    Fiber and Neofiber, the muskrats.
Insectivora, many scattered examples, as —
    Myogale, the desman.
    Crossopus (Sorex) the water-shrew.
    Neosorex, the American water-shrew
    Chimarrogale.
    Nectogale.
    Potamogale.
    Limnogale.
Ungulata,
  Artiodactyla,
    Hippopotamus.
Marsupiala,
    Chironectes, the water-opossum.
Monotremata,
    Ornithorhynchus.

Besides these there might be mentioned among extinct forms the Zeuglodontidæ, thoroughly aquatic animals doubtfully related

to the Cetacea, or according to some authors, to the Pinnipedia ; the oreodont Merycochœrus, probably semi-aquatic, the creodont Patriofelis, a possible ancestor of the Pinnipedia, and the extinct rhinoceros, *Metamynodon planifrons* Scott and Osborn, which, though related to modern species which are not aquatic, had the shorter nasals, more dorsal external nares and more dorsally curved ribs which mark many aquatic forms, as will be shown later.

That many forms have but recently become aquatic is certain in such as have undergone little or no modification in structure, while others must have assumed aquatic life in very remote times if the amount of the adaptation to the environment is any criterion. Kükenthal points out that the amount of adaptation depends upon the length of time during which the influence of the water has been operating and upon the amount of connection retained with the land, and that we can assign the relationships of aquatic mammals with certainty in proportion to the time that has elapsed since they were separated from their terrestrial relatives. For example, we know definitely the relationships of the forms that have recently taken up the aquatic habit, such as the otters, muskrats, etc., of the Pinnipedia we know that they are Carnivora, of the Sirenia we know almost nothing (according to various authors they have been held to show relationships with the Ungulata, which view the evidence largely favors, the Cetacea, or to form an entirely distinct stem.), and as to the Cetacea we are absolutely in the dark. Kükenthal even maintains that the latter group is diphyletic from quite different sources and that the supposed relationships between the Odontoceti and the Mystacoceti are merely parallelisms due to similarity of environment. The reason for this is to be found in the profound modification resulting from life in the water which affects internal as well as external structures and leads to parallelisms in many structures in forms not genetically related.

For convenience in treatment, the various adaptations may for the most part be roughly classified in three groups as follows : — I. Adaptations connected with the general body form including those of the head, trunk and tail regions. II. Those affecting the limbs. III. Those affecting the integument.

I. The tendency of the body to take on a "fish-like" form is too well known to need any discussion, as it goes without saying that such a form is best adapted to progress in the water. It is most marked in such animals as are most aquatic, as the Cetacea, Sirenia and Pinnipedia, and to a less extent in other forms as Enhydris, Potamogale, etc. The anterior part of the body tends to become more rigid and concentrated, especially in the cervical region, while the posterior part of the body becomes more mobile for purposes of propulsion.

In the head there is found in the Cetacea and the extinct zeuglodonts a lengthening of the face with a shortening of the cranium. In the most extreme cases the head is nearly one third the length of the body. In the Sirenia the face is somewhat elongate, but not excessively so, while in the Pinnipedia it is never very elongate and may be quite short, while the cranium is broad and flat. The length of the head is conditioned so largely by the length of the jaws that it would seem that its shape is not a result merely of life in the water, so much as of adaptation to certain kinds of aquatic food. The secondary simplification of the teeth which takes place in all truly aquatic mammals must also be connected with food conditions. In the Mystacoceti the teeth are never functional but are present only in the embryo and are absorbed before birth and replaced by whalebone. As the food consists of very minute forms the adaptation is evident. In the Odontoceti or toothed whales the teeth are purely raptorial in character, simple and fang-like and often retroverted, and admirably adapted for the capture of the food, which in most cases consists of cephalopods, crustaceans and fishes. The number of teeth may be greatly increased as in Globiocephalus where the total number may be over 100, and even twice that number may be found in Delphinus and Inia, or the number may be greatly reduced as in Monodon and Ziphius, or the teeth may be vestigial as in Hyperoodon. In the extinct zeuglodonts the teeth had not become so simplified, as they still possessed two roots and a crenulated crown. This "zeuglodont" condition of the teeth is found at the present time in the majority of the Pinnipedia. In the herbivorous Sirenia the teeth when present are of the bilophodont type, undoubtedly adaptive

to the food, which consists of aquatic plants. In the recently extinct genus Rhytina the teeth are absent and are replaced by horny plates. In the manatee they are secondarily increased in number. Along with the simplification of the dentition is found occurring a great simplification of the jaws, particularly the lower which tends toward the loss of all prominences for the attachment of muscles, so that in the Cetacea the coronoid process is often greatly reduced and the angle as well. The articulation with the squamosal becomes loose and simplified, and the symphysis does not ankylose except in a few cases such as Platanista. Even in some of the Pinnipedia there occurs a noticeable weakening of the jaw and looseness of the symphysis. However, in the walrus whose food consists chiefly of bivalve molluscs, the teeth are adapted to crushing the shells and the jaw is remarkably heavy and strong and in the adult the symphysis is thoroughly ankylosed. The crushing jaw of the Sirenia is also ankylosed. In general the pterygoid processes also tend to become reduced, and there is a tendency toward a looseness of articulation in all the bones of the head, particularly in the Cetacea.

The shifting of the external nares from a terminal into a more dorsal position is an adaptation to breathing at the surface of the water. This is accomplished by a shortening up of the nasal bones, which in the Cetacea become merely vestiges on the anterior surface of the frontals. In the Cetacea the opening is so shifted as to lie quite on top of the head, while in the Sirenia and Pinnipedia also the shifting is quite noticeable. It is a noteworthy fact that the true seals, Phocidæ, and the dugong, Halicore, which give other indications of a longer life in the water than the eared seals, Otariidae, and the manatee, Trichechus, respectively, have the external nares also more dorsal. The hippopotamus and the extinct rhinoceros, *Metamynodon planifrons*, also show a somewhat dorsal position of the nares. In many cases the external narial opening can be closed to exclude the water, as in Sirenia and Cetacea. In the Odontoceti the two external nares fuse into a single opening before reaching the surface, a condition paralleled by some of the crocodiles.

The internal nares are also shifted backward to bring the

opening more nearly over the epiglottis, and along with this in the Cetacea is found an intranarial epiglottis [1] formed by the prolongation upward of the epiglottis and the arytenoid cartilage into the nostril, forming an independent continuous passage from the exterior to the lungs. These are undoubtedly adaptations to the capture of food in connection with conditions of respiration at the surface of the water and permit of food being held in the mouth or even of being swallowed without interfering with respiration. In the Cetacea, naturally, the process is carried farthest, and here the extreme is found in such forms as Globiocephalus in which the postnarial opening is secondarily bridged over by the pterygoids and the palatines are entirely excluded from the anterior border. In Delphinapterus the palatines take part for a small space in the formation of the anterior border of the opening, and from this condition we find successive steps to that found in the less modified forms, as the Pinnipedia, where the whole border is formed by the palatines. The palatines are posteriorly elongated as the first step in the backward shifting of the internal nares, as shown by the Pinnipedia, Ornithorhynchus, etc. The reduction of the salivary glands is also to be noted. As the function of the saliva is chiefly a mechanical one connected with deglutition the reduction of the glands in forms taking their food in the water is easily explained.

The loss of the external ears is another noticeable result of aquatic life. In the Cetacea, Sirenia and Phocidæ the external ear is lost entirely, and among the eared seals, Otariidæ, it is found in various stages of reduction. The opening of the ear is often valvular so that it can be closed when in the water, and this condition occurs even among those forms which are only semi-aquatic, as in Crossopus and Neosorex. There is a tendency among certain forms, also, toward the arrangement of the ears, eyes and external nares in one plane near the top of the head so that all may come into use at once without exposing very much

[1] Possibly this is to be looked upon as the persistence of a larval structure, as Howes has found an intranarial epiglottis in the young of a number of the more primitive mammals having a forced lactation by means of mammary muscles, and it is perhaps more than a mere coincidence that the whales have also a forced lactation.

of the head. This is most marked in the hippopotamus but is seen also in the capybara and beaver and other forms. In such forms the eye-sockets may be quite prominent.

The shortening of the neck is another manifestation of the tendency to take on a "fish-like" form, in connection with the question of locomotion. In all truly aquatic forms this is noticeable. It is brought about by a great shortening up of the cervical vertebræ, and in extreme cases the loss of a vertebra (manatee) or the fusion of some or all of the cervical vertebræ may take place (most Cetacea). The occipital condyles also tend to become flattened out and the odontoid process is reduced. The final result of this process is an almost complete lack of motion between the head and trunk, a condition finding its parallel in the fishes, ichthyosaurs and other truly aquatic forms. This loss of motion in the cervical region is more than compensated for, however, by the greatly increased power of motion attained by the more posterior portion of the body. Here the intervertebral connections are simplified and the vertebral column rendered more mobile, since for the purpose of swimming, mobility of a certain sort in the posterior part of the body is most useful. The zygapophyses are progressively reduced and lost posteriorly in the Sirenia and Cetacea, and other processes such as anapophyses are entirely lost. Also the pleurapophyses or ribs of the sacral region are lost as the pelvis loses its connection with the sacrum (Sirenia and Cetacea). The spinous processes tend generally to reduction, as in the cervical and anterior dorsal region there is no need for the strong supporting muscles and ligaments of terrestrial forms, and connections for leaping muscles are lost posteriorly. The spinous processes of the posterior body region and anterior caudal region seem to be secondarily elongated, probably in connection with the up and down motion of the tail in swimming, in many Cetacea, and the chevron bones of the anterior caudal region in some forms are also elongated. The centra of the vertebræ become amphiplatyan in the Sirenia and Cetacea throughout most of the column, and the intervertebral cartilages become thicker especially posteriorly. The epiphyses, also, tend to unite at a very late period.

In all truly aquatic mammals the thorax takes on a character-

istic cylindrical form, there being little or none of the lateral compression such as is common among land forms, and this seems to be the first step in the enlargement of the chest capacity, as it is found in Pinnipedia as well as in the Sirenia and Cetacea. The ribs at first tend to become highly arched dorsally and then to move upward in their point of attachment from the centra to the transverse processes. The beginning of this process is found in the Pinnipedia and its culmination is seen in the whalebone whales, Balænoidea, where all the ribs are attached only to the transverse processes of the vertebræ. Possibly this is of service in equilibration as the lungs can take a more dorsal position. Accompanying these changes the diaphragm becomes much more oblique and much more strongly muscular, undoubtedly giving greater control over the chest capacity in the peculiar conditions of respiration necessarily accompanying aquatic life.

Perhaps the most striking external adaptation to aquatic life is the assumption of "fins" for use in swimming. Many of the Cetacea have developed a fleshy dorsal fin which undoubtedly serves the same purpose as the similar organ among the fishes and ichthyosaurs. The Sirenia and Cetacea have a large expanded caudal fin supported by a dense framework of connective tissue and used as a propeller in swimming. This organ differs from that of the fishes in being expanded laterally instead of vertically, and this arrangement of the fin permits the animal to rise to the surface more quickly for air and to dive again as readily, and it accounts for the peculiar undulatory motion so noticeable in these animals when they are swimming at the surface. The flukes of the tail are said to be capable of a somewhat rotary sweep like the blades of a screw propeller at each stroke of the tail. It is a noteworthy fact that nearly all aquatic mammals have this dorso-ventral flattening of the tail, the only exceptions being Potamogale, Myogale and the muskrats, Fiber and Neofiber which have the tail expanded vertically after the manner of a salamander. Potamogale is said to swim like a newt with the legs folded against the body, and to be an exceedingly rapid swimmer. The tail is so large and strong and functions so completely as a propeller that the limbs have not been modified even to the extent of webbed toes although the

animal is quite aquatic in its habits. In Chimarrogale, Nectogale and Crossopus there is a stiff fringe of hairs which may serve the same purpose as the compression of the tail. The caudal vertebræ are flattened laterally in Ornithorhynchus, Castor, Halicore, and some Cetacea.

II. In the limbs, which at first play such a part in locomotion in the water, we should expect to find marked adaptation. Naturally those forms which move about occasionally upon the land have the limbs less modified than those which have become more completely aquatic, as progress upon the land calls for an entirely different form of limb from that which is most useful in the water. In some animals semi-aquatic habits have been assumed while as yet no modification of the limb has taken place. Thus in the water-vole, *Microtus amphibius*, there is no trace of a web connecting the toes. Some other forms, as the muskrats, have only rudiments of webs at the base of the toes, while the minks have the toes partially webbed. The beavers and the water-opossum, Chironectes, have the hind feet large and fully webbed, while in the otters, the sea-otter and the duck-bill, Ornithorhynchus, both feet are webbed to the claws. In the more completely aquatic Pinnipedia the membranes, supported by connective tissues, reach beyond the digits, but the claws are still present. In the Sirenia the whole forearm becomes enclosed in the membrane and the last vestiges of the claws are seen. The manatee retains slight vestiges of three nails, (*T. inunguis* questionably), but the dugong and the extinct Steller's sea-cow, *Rhytina stelleri*, lack the nails entirely. The whales reach the climax of modification, as all of the limb outside of the body becomes enveloped, and the nails are entirely lost (Leboucq has described the nails in the embryo). The limb now becomes simply a balancing organ and the transition from an ambulatory to a natatory limb is complete. Kükenthal aptly says, "In exact ratio to the adaptation to aquatic life do we find the membranes just indicated or uniting the digits or enveloping them entirely." In lieu of webbing there is sometimes developed a stiff fringe of bristly hairs on the margins of the feet as in Crossopus. This may be carried still farther by the addition of a fringe of hairs on the sides of all the toes, as

in Chimarrogale, or in addition to the fringes the foot may be widened by disc-like pads and at the same time be webbed as in Nectogale and Myogale.

Another transformation due to life in the water is found in the shortening of the arm and forearm and lengthening of the digits. This begins in the Pinnipedia where the arm is considerably reduced in length though it is still serviceable to some extent in locomotion and in most cases capable of supporting the weight of the body. In the Sirenia and Cetacea, where progress upon the land has been entirely given up, the arm is still more reduced and in the latter group may be entirely withdrawn into the body wall, only the hand remaining outside to form the fin. In both these groups, but in the latter especially, the arm no longer functions as a propelling organ but serves, as in most fishes, merely as a balancing organ, the greatly developed tail furnishing the motive power. The extreme of adaptation in the hand is reached in the addition of extra phalanges in the digits, hyperphalangy, and the addition of an extra digit, hyperdactyly, thus increasing the extent of the hand. Hyperphalangy is common among the Cetacea, where as many as twelve phalanges may occur in a single digit, and even a greater number than this in one species, *Globiocephalus melas*. It apparently does not occur in other aquatic mammals except occasionally an extra phalanx may be found in Sirenia, but a close parallelism is seen in the ichthyosaurs and plesiosaurs. Kükenthal accounts for hyperphalangy as a result of retarded ossification and the formation of double epiphyses. These epiphyses tend to ossify at later and later periods and finally to become entirely separate bones forming the extra phalanges. As compared with other theories that have been advanced to account for hyperphalangy, this theory of Kükenthal, strengthened by the array of facts which he brings to its support, seems most reasonable and sufficient to account for the conditions in the Mammalia at least. Hyperdactyly is not common in the Mammalia but it is known to occur in some of the Cetacea, *e. g. Delphinapterus leucas*, the white whale, by a splitting of the fifth digit, as shown by Kükenthal and Leboucq. In the ichthyosaurs the process went much farther, several secondary digits being formed.

Along with the change of function in the anterior limb occurs the absence of clavicles, the reduction of the sternum and the reduction and loss of articulation between the bones of the limb. The distal elements, carpals and phalanges, tend to become separated and imbedded in cartilage so that there is only a general flexibility of the hand, but the humerus, radius and ulna become exceedingly short and lose all motion upon each other so that there is not only no torsional motion of the radius and ulna but also no motion in the elbow joint. As a final expression of this the three bones often become ankylosed at the elbow in the Cetacea. There is also a noticeable flattening of the bones (the humerus is flattened distally only) and, connected with the change in function of the limb, there is a reduction of prominences for the attachment of certain muscles. Thus in the Sirenia and Cetacea the deltoid crest and the olecranon process become very much reduced. The entepicondylar foramen is also absent. The spreading out of the ulna and radius permits the intermedium to move up well between the distal ends of these bones in some of the Cetacea, a condition not found in any other group of mammals but paralleling the condition in Amphibia and many reptiles. The elongated sickle-shaped hand of Globiocephalus and some other cetaceans is paralleled by that of the Thalattosuchia and Ichthyosauria among the reptiles.

In the hind limb the story is somewhat different, according to whether or not the form in question possesses a tail fin. In the Sirenia and Cetacea which have this organ there is no function remaining for the hind limbs, as the balance can be preserved by the anterior limbs and the tail furnishes the motive power, and as a result the hind limbs are entirely lost, with the exception of the merest vestiges of the skeletal structures which have lost all connection with the vertebral column and are not at all visible externally. The reduction process in the pelvis begins even in the seals as the ilium never unites solidly with the sacrum as it does in land forms. In all the Pinnipedia, a tail fin not being present, the hinder limbs have gradually moved backward to assume the function of a propeller and a motion somewhat similar to the tail of the cetacean. In the Phocidæ, the true seals, this process has gone so far that the limbs have become quite bound

up with the tail and are entirely useless for locomotion on the land. It was this similarity in action and arrangement that led Ryder in 1885 to derive the flukes of the tail in the Cetacea and Sirenia from the hinder limbs, — a position no longer tenable, as they are in no sense homologous. In the hair seals, Otariidæ, and walrus, Trichechidæ, the hinder limbs have not undergone so much modification and are capable of being turned forward in progression on the land, in which operation they are functional to some extent. With the change from the ambulatory to the natatory limb there comes about necessarily a great change in the musculature of the limb.

III. The changes connected with the integument may be noted as follows, — loss of hair, acquisition of blubber, loss of the integumentary glands, smooth muscles and nerves of the skin, and loss of dermal armature. The loss of hair is usually not marked in those forms which spend only a portion of the time in the water, but in the more completely aquatic forms there is almost an entire absence of it. In the "hair seals," Otariidæ, which are the least aquatic of the group, there is a fairly good coat of hair, and in the case of the fur-bearing species this is intermingled with a dense coat of fine fur, but in the walruses, Trichechidæ, and "true seals," Phocidæ, there remains only short, appressed, coarse hair. In the hippopotamus and the Sirenia there remains but very little hair in the adult, and again in the Cetacea we find remaining usually only the merest vestiges and sometimes these occur only in the embryo. Kükenthal has pointed out that all these forms are distinctly more hairy in the embryo than in the adult (except in the case of the white whale, Delphinapterus, and the narwhal, Monodon, which have lost all traces of hair even in the embryo), thus showing their origin from forms that were more hairy. The acquisition of blubber goes on *pari passu* with the loss of hair, until in the Cetacea the blubber becomes extremely thick. Kükenthal is responsible for the statement that in the seals "hand and hand with the biological observation of the longer or shorter time spent on land by the various species, we can determine the presence of a denser covering of hair or detect a thinning of the coat, corresponding with the gradual increase of

the layer of blubber." The reason for this is to be found in the fact that hair is but a poor defense against the loss of heat when in the water, while the layer of oil constituting the blubber affords an excellent protection. Accompanying the loss of the hair we naturally find also a reduction in the sebaceous glands, smooth muscles and nerves of the skin. The sweat glands are also wanting in the Sirenia and Cetacea.

There are indications that the toothed whales, Odontoceti, have been derived from forms possessing a dermal armature. Kükenthal, to whom this observation is due has shown that in Neomeris there remains in the adult considerable vestiges of what must be looked upon as a dermal armor. This has been preserved usually only in those regions of the body where it may be useful as a protection, as on the anterior margin of the flippers, the anterior dorsal region and around the blow-hole, though traces may occur on other parts of the body. The study of the embryo shows that this is only a remnant of what was once a much more extensive dermal armor. In the porpoises is found the last appearance of this armor in the tubercles along the dorsal fin. Here also they are more abundant in the embryo. It is worthy of note in this connection that there have been found with the extinct zeuglodons certain ossicles which indicate a more extensive armor than is known to occur among recent whales. The loss of armor is paralleled a number of times in the marine reptiles. In the ichthyosaurs, the most aquatic reptiles known, Fraas has shown that the dermal armor was almost entirely lost, being retained only along the anterior border of the fore limb, — the same position in which it occurs in Neomeris.

Besides the adaptations already mentioned, it may be noted that the bones of the truly aquatic forms are light and spongy, particularly in the Cetacea, and in this group also the bones become impregnated with oil. In the Sirenia the bones are exceedingly dense and heavy, but in explanation of this it must be remembered that these forms are not pelagic but live along the shore in shallow water and find their food in the sea-weed growing upon the bottom. The very heavy skeleton seems to be an adaptation to bottom-feeding habits. In support of this

view it may be added that the walrus, which is a bottom-feeding form living chiefly upon bivalve molluscs, has the skeleton noticeably heavier than that of any other of the Pinnipedia which are generally piscivorous in habit.

The kidneys of most aquatic mammals are lobulated, Hippopotamus, Pinnipedia, Cetacea, but how this is to be explained by aquatic life is not clear.

The testes are retained within the abdomen in the Cetacea, Sirenia and the true seals, Phocidæ. In the less aquatic hair seals, Otariidæ, they are scrotal as in the majority of mammals.

Retia mirabilia, anastomoses of smaller arteries and veins, are abundantly developed in the Sirenia and Cetacea. These cause a slowing down of the blood stream and it has been suggested that this is connected with the oxidation of the blood in these forms that breathe infrequently.

In the foregoing enumeration of adaptations the writer has attempted to include only those that seem to be a result of aquatic life, but in certain instances these may be open to question. For example, Beddard has been inclined to question the loss of hair in the Cetacea and Sirenia as due to aquatic life, holding out the suggestion in the case of the whales that they have probably been derived from armored forms in which the hair was already lacking. That the Odontoceti have probably been derived in this way is true and it is also true that they have less hair than other marine forms, but it is equally true that hairs have been found, at least in the embryo, in all but a few species and in all cases these hairs are degenerate or vestigial in nature. The inference seems plain that the ancestors of these forms had these hairs better developed. As to the Mystacoceti and the Sirenia, which are almost equally devoid of hair, there is not the slightest evidence that they have been derived from armored forms. On the contrary it has been shown that in the embryo these forms are distinctly more hairy. This evidence taken in addition to the progressive degeneration of the coat observed in the Pinnipedia makes the reduction of the hair by aquatic life strongly probable.

In general it may be said for any character that when the same tendency is observed in two such widely separated groups

as the Sirenia and Cetacea (and the latter group is almost certainly diphyletic) it would seem difficult to explain on any other ground than similarity of environment. When a third group, as the Pinnipedia, shows the same tendency the matter becomes almost a certainty.

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